Coral communities in extreme environmental conditions in the Northern Territory, Australia

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Abstract

An extensive intertidal reef flat in the macro-tidal marine waters of the Northern Territory was chosen to investigate species composition and zonation persisting under extreme environmental conditions. Thirty-six visual belt transects were used to quantify scleractininan corals, benthic algae and other sessile invertebrates which varied in vertical and horizontal space. Thirty-four coral species were identified. Most species were represented by the family Merulinidae, with lifeform characteristics typical of species specialised in environmental tolerance to high sedimentation, turbidity and temperature (i.e. massive, sub-massive and encrusting growth forms with convex and steep sided morphologies, thick skeletal tissue and large polyps). Whilst the combination of environmental and ecological characteristics of this reef flat community can be viewed as distinctive to the Darwin region, a number of similarities can be compared to reef communities reported in extreme environments of the Arabian Gulf, Red Sea and other regions of tropical northern Australia.

Introduction

Coral communities which presently persist in extreme environmental conditions are of contemporary interest towards understanding species resilience and potential for adaptation to climate change (Hughes *et al.* 2003; Bauman *et al.* 2011, 2013a, 2013b; Dandan *et al.* 2015). Predictions for climate change stressors for coral communities include warmer sea temperature and changes in extreme episodic events such as heavy rainfall, storms and possible sediment and nutrient debouching from rivers and run-off (Gilmour *et al.* 2006). Such environmental perturbations are known to be associated with mass coral bleaching and sudden die off (Glynn 1993; Depczynski *et al.* 2013). Coral species of the coastal waters in the vicinity of Darwin Harbour, Northern Territory (Wolstenholme *et al.* 1997), the Kimberley coast, northwestern Australia (Dandan *et al.* 2015; Schoepf *et al.* 2015) and the Arabian Gulf (Sheppard & Sheppard 1991; Coles 1997; Coles 2003; Riegl 1999; Bauman *et al.* 2011; Riegl & Purkis 2012) survive in harsh conditions and offer insight to species with high climatic tolerances and adaptation.

Climatic trends in this region of Australia are changing. Since 1950, the Northern Territory average rainfall has risen 35.7 mm per decade during November–April and fallen 0.4 mm per decade during May–October. From 1910 to 2003, the intensity of heavy daily rainfall gradually rose by 10% (Hennessy *et al.* 2004). Water temperatures at the shoreline may reach over 36°C at high tide, with tide pools and standing water bodies reaching over 43 °C at low tide which is similar to the high temperature fluctuations in the Arabian Gulf, and well above temperature ranges corals traditionally considered limiting to coral survival (Coles 1997). Sea surface temperatures north of Australia have been at record-breaking highs. In 2010, temperatures north of Australia broke previous records by large margins and were also above average during the 2011–2012 La Niña event (Australian Bureau of Meteorology 2013).

An extensive intertidal reef flat community off the north-eastern shoreline of Darwin Harbour was chosen to investigate coral zonation on a macro-tidal shoreline. The marine waters of Darwin Harbour are subjected to daily and seasonal fluctuations in sea surface temperature, light availability and extreme levels of sedimentation and turbidity which provides insight to northern Australian coral species that have already adapted to extreme climatic conditions.

Methods

Study site

Nightcliff Reef (Fig. 1) was surveyed at low spring tide between September and October 1994. Darwin Harbour is a ria coast formed by the post-glacial marine flooding of a dissected plateau. Subsequent sedimentary infill has resulted in the formation of numerous embayments, islands and extensive mangrove-vegetated tidal flats (Semeniuk 1985). The dominant lithological type is ferricrete laterite with phyllite/siltstone and this is reflected by the presence of conspicuous medium to coarse grained lateritic pebbles of the upper beach sediments. The coral community at Nightcliff exists as a veneer reef by colonising hard substrates of rock and consolidated materials without accreting substantial calcium carbonate substrata (Hooper 1987; Mitchie 1987). The community extends seaward to a distance of approximately 500 m from the shoreline at low spring tide.

Tides in Darwin Harbour exhibit semidiurnal inequality with a spring tidal range is in the vicinity of 0.1–7.8 m. Tidal currents are very strong ranging from 0.25–1.4 m/s and recording as high as 2 m/s (Semeniuk 1985). The concentration of rivers, streams and creeks with accompanying discharge, and the strong tidal movement of the system, account for excessive sediment mixing and high turbidity (Michie 1987). Nightcliff Reef is fully emersed for 2–3 hours during low spring tides that are less than 1 m. Low spring tides occur between 1100–1600 hrs in the period September to March (wet season) and between 2300–0400 hrs in the period April to August (dry season).

Stratification

A topographic contour map of the reef was generated from random spot heights measured using a digital theodolite. All heights were referenced from a survey datum

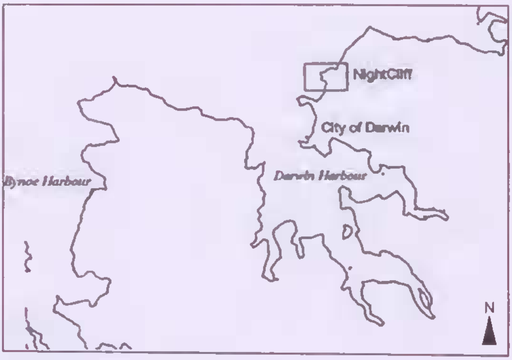

Fig. 1. Location of Nightcliff Reef off the north-eastern foreshore of Darwin Harbour.

point adjacent to Nightcliff Pier, and were converted to metres above the lowest astronomical tide (i.e. 0 m). The contour map was used to stratify the reef into three main vertical zones: (1) the upper reef flat which occupied a vertical height between 1.4–1.8 m; (2) the middle reef flat between 0.9–1.4 m; and (3) the lower reef flat between 0.3–0.9 m.

Sampling

Sampling was conducted using four replicate 1 m x 20 m contiguous belt transects that were haphazardly placed in each of the upper, middle, and lower reef flat vertical zones The sampling was repeated in three localities (north, central and south locations) to account for any variations in substrata micro-topography, sediment deposition and taxa composition that may occur horizontally across the reef relative to the shoreline. In total, 36 belt transects were surveyed. Contiguous belt transect was chosen as the sampling unit to improve the recording of small and less abundant species, and representation of microhabitats (e.g. large or small coral colonies, sand patches, tide pools) in any given zone and locality (Chiappone & Sullivan 1991; Sullivan & Chiappone 1992). Species abundances of all sessile taxa were recorded by visual estimates of percentage cover and numbers of individuals for each 1 m^2 quadrat. Lifeform attributes of coral colonies were recorded using categories of English *et al.* (1994). When a particular species was encountered that could not be identified in the field, a sample of the species was collected for identification in the laboratory and also compared to collection specimens held at the Northern Territory Museum. Original taxonomic identifications for scleractinian corals followed that of Veron and Pichon (1976, 1980, 1982); Veron *et al.* (1977); Veron and Wallace (1985) and Veron (1986). Algal identifications followed that of Jaasund (1976); Cribb (1983); Cribb and Cribb (1985); Lawson and John (1987) and Price and Scott (1992). Updates to recent taxonomic revisions follow Wynne (2011); Budd *et al.* (2012); Guiry and Guiry (2013); Huang *et al.* (2014) and WoRMS Editorial Board (2015). All data presented in the text and figures are the arithmetic mean.

Results and Discussion

A total of 75 sessile species comprising scleractinian corals, algae, and sessile invertebrates were identified in the 36 transects sampled across the upper, middle and lower reef flat zones. 34 species of scleractinian corals from eight families were recorded (Table 1). The majority of species were members of the family Merulinidae, represented by 18 species (or 53% of all corals), followed by the Lobophyllidae and Poritidae, each represented by 4 species (23% of all corals). All remaining 5 families were represented by 1 or 2 species (24% of all corals). The more abundant corals, all with greater than 2% in mean percentage cover pooled for all 36 transects, were *Platygyra sinensis* (Fig. 2), *Porites* cf *nigrescens, Astrea curta*, *Coelastrea aspera* and *Goniastrea retiformis.* Secondary dominant corals (1–2%) were *Porites lutea, Lobophyllia hemprichii*, *Platygyra daedalea*, *Galaxea astreata*, *Favites*

Fig. 2. Massive colony of *Platygyra sinensis* at Nightcliff Reef, Darwin Harbour. This particular species and *Coelastrea aspera* have been sighted attaining colony sizes of up to 1.8 m in height. (Lawrance Ferns)

Table 1. Mean percentage cover of scleractinian corals, algae, other sessile invertebrates and physical substrates at Nightcliff Reef. Lifeform categories M = massive, S = submassive, E = encrusting, D/C = digitate/coryombose, R = ramose, T = turf, BF = bladed foliose, F = foliose, EC = erect coralline.

Family	Species	Lifeform	Upper Reef Flat (>1.4–1.8 m)			Middle Reef Flat (>0.9–1.4 m)			Lower Reef Flat (0.3–0.9 m)		
			north	central	south	north	central	south	north	central	south
CORALS											
Merulinidae	*Platygyra sinensis*	M		0.01		0.21		0.21	19.60	4.13	1.48
Poritidae	*Porites cf nigrescens*	S/R				8.10			4.34	5.76	3.75
Merulinidae	*Astrea curta*	M		0.06		2.85	0.15	1.66	3.93	3.25	2.35
Merulinidae	*Coelastrea aspera*	M							2.20	2.84	0.60
Merulinidae	*Goniastrea retiformis*	M	0.03	0.18	0.24	0.20	0.04	0.08	2.80	0.46	0.11
Poritidae	*Porites lutea*	M				0.50				1.36	
n/a	*Dead standing coral*	n/a				0.45			0.61	0.46	0.34
Lobophylliidae	*Lobophyllia hemprichii*	S							1.79		
Merulinidae	*Platygyra daedalea*	M				0.23			1.19	0.26	0.11
Euphylliidae	*Galaxea astreata*	E				0.13			1.24	0.25	
Merulinidae	*Favites abdita*	S				0.30	0.03		0.60	0.43	0.15
Merulinidae	*Dipastrea speciosa*	M	0.20	0.05		0.32		0.03	0.28	0.34	0.04
Merulinidae	*Dipastrea rotumana*	M				0.23			0.48	0.14	0.09
n/a	*Juvenile corals*	n/a	0.11	0.08		0.09		0.06	0.32	0.16	0.09
Merulinidae	*Dipastrea matthaii*	M				0.15			0.33	0.08	0.04
Merulinidae	*Dipastrea amicorum*	M	0.03			0.13			0.09	0.29	0.04
Merulinidae	*Cyphastrea serailia*	E	0.06	0.05		0.13	0.05		0.01	0.13	
Merulinidae	*Dipastrea favus*	M	0.12	0.04		0.17			0.03	0.05	
Acroporidae	*Acropora millepora*	D/C							0.34	0.05	
Merulinidae	*Dipastrea pallida*	M	0.01	0.10		0.16				0.04	
Poritidae	*Porites sp.1*	M				0.24		0.03			
Poritidae	*Goniopora cf. lobata*	S				0.04			0.14	0.09	
Lobophylliidae	*Symphyllia recta*	M				0.01			0.23		
Acroporidae	*Montipora encrusting*	E							0.13	0.06	
Dendrophyllidae	*Turbinaria mesenterina*	E				0.03			0.10		
Dendrophyllidae	*Turbinaria conspicua*	T							0.10		
Merulinidae	*Merulina ampliata*	E							0.10		
Scleractinia incertae sedis	*Leptastrea purpurea*	E								0.09	
Lobophylliidae	*Echinophyllia aspera*	E							0.09		
Scleractinia incertae sedis	*Leptastrea transversa*	E	0.01		0.01	0.02	0.01		0.00	0.03	
Merulinidae	*Cyphastrea microphthalma*	E							0.08		
Merulinidae	*Goniastrea pectinata*	E				0.03			0.04		

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Family	Species	Lifeform	Upper Reef Flat (>1.4–1.8 m)			Middle Reef Flat (>0.9–1.4 m)			Lower Reef Flat (0.3–0.9 m)		
			north	central	south	north	central	south	north	central	south
Merulinidae	*Cyphastrea chalcidicum*	E								0.05	
Psammocoridae	*Psammocora contigua*	S				0.03					
Merulinidae	*Goniastrea favulus*	M							0.03		
Lobophylliidae	*Moseleya latistellata*	E							0.01		
Subtotal: Corals			0.57	0.57	0.25	14.75	0.28	2.07	41.23	20.80	9.19
ALGAE											
Sargassaceae	*Sargassaceae Holdfasts*	BF	4.01	0.43			1.81	0.08			
Dictyotaceae	*Padina australis*	F	12.55	20.39	6.84	0.03	0.63	0.15			0.03
Galaxauraceae	*Tricleocarpa fragilis*	T	0.16	0.61	0.69		0.23	0.01			
Dictyotaceae	*Dictyopteris sp.*	BF	0.09	1.16			0.01				
Corallinaceae	*Amphiroa fragilissima*	T					2.72	0.23			
Sargassaceae	*Sargassopsis decurrens (Sighted only)*	BF									
Rhizophyllidaceae	*Portieria hornemannii*	T	1.21	0.24	0.05		0.30	0.20			
Dictyotaceae	*Spatoglossum asperum*	BF	0.32	1.24							
Halimedaceae	*Halimeda cf tuna*	EC	0.01		0.01		0.12				
Rhodomelaceae	*Palisada perforata*	T	0.11	0.21	1.21						
Rhodomelaceae	*Digenea simplex*	T									
Cystocloniaceae	*Hypnea spinella*	T	0.28		0.08						
Rhodomelaceae	*Acanthophora spicifera*	T	0.12	0.13	0.86		0.11				
Gracilariaceae	*Gracilaria salicornia*	T	0.28	0.33	0.61						
Halimedaceae	*Halimeda opuntia*	EC	0.13	0.21	0.01		0.27	0.11			
Anadyomenaceae	*Anadyomene plicata*	EC	0.22	0.21	0.07		0.26	0.33			
Cystocloniaceae	*Hypnea valentiae*	T	0.24	0.10	0.45						
Scytosiphonaceae	*Hydroclathrus clathratus*	T	0.08	0.51	0.13						
Caulerpaceae	*Caulerpa lentillifera*	F			0.01		0.08				
Rhodomelaceae	*Laurencia majuscula*	T		0.04	0.09						
Rhodomelaceae	*Laurencia intricata*	T		0.12	0.05		0.17				
Rhodomelaceae	*Tolypiocladia sp.*	T	0.01	0.01	0.22		0.09				
Callithamniaceae	*Crouania attenuata*	T	0.01	0.03	0.29						
Caulerpaceae	*Caulerpa racemosa*	F					0.03				
Galaxauraceae	*Dichotomaria obtusata*	T									
Caulerpaceae	*Caulerpa serrulata*	F	0.04								

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Family	Species	Lifeform	Upper Reef Flat (>1.4–1.8 m)			Middle Reef Flat (>0.9–1.4 m)			Lower Reef Flat (0.3–0.9 m)		
			north	central	south	north	central	south	north	central	south
Gelidiellaceae	*Gelidiella acerosa*	T	0.08	0.05	0.03						
Rhodomelaceae	*Laurencia obtusa*	T	0.05		0.04						
Cystocloniaceae	*Hypnea pannosa*	T				0.02			0.03		0.02
Cystocloniaceae	*Hypnea cornuta*	T			0.02						
Ulvaceae	*Ulva intestinalis*	F	0.03		0.02						
Champiaceae	*Champia parvula*	T					0.04				
Pithophoraceae	*Dictyosphaeria cavernosa*	F		0.04							
Cystocloniaceae	*Hypnea cf hamulosa*	T			0.03						
Soheriaceae	*Sarconema filiforme*	T	0.01		0.01						
Dichotomosiphonaceae	*Avrainvillea erecta*	F						0.01			
Dasycladaceae	*Neomeris annulata*	F	0.01								
Dictyotaceae	*Dictyota bartayresiana* (Sighted Only)	BF									
Sub-total: Algae		20.05	26.06	11.82	0.05	6.87	1.12	0.03		0.05	
SESSILE INVERTEBRATES											
Sponges		0.25	0.28	0.03	17.58	2.63	0.09	0.48	0.08	0.04	
Other fauna (ascidians, soft corals)				0.03		0.04				0.01	
BARE SUBSTRATES											
Coarse sand			2.84	11.79		57.40			5.26	3.46	4.06
Coral rubble						6.90			53.01	75.67	86.84
Muddy Rock			72.88	55.93	74.51		82.09	78.12			
Muddy Sand			3.54	5.48	13.41	3.31	8.15	18.59			
Total (% Cover)			100	100	100	100	100	100	100	100	100

abdita, Dipastrea speciosa, and *Dipastrea rotumana.* Corals with 'massive' and 'sub-massive' lifeforms were the most common growth morphologies with 20 species (or 59% of all corals). The other main lifeform was 'encrusting' comprising 12 species (35% total of all corals). Only one species with digitate and tabulate lifeform categories were recorded (6% of all corals).

Coral abundance and species richness varied between vertical zones and horizontal localities across the reef. Physical factors such sediment type, micro-topography, standing water, with the relative influence of each factor shifting between and within vertical zones and localities, is the likely cause of the observed variation (Table 1). Species cover and richness increased markedly seaward from the upper reef flat zone (1.4–1.8 m) to the lower reef flat zone (0.3–0.9 m) which has the highest coral abundance and species richness. This is consistent with similar studies that have found intertidal corals to be more successful below 1 m tidal height elevations and reaffirms the period of emersion time is an important factor determining the their upper vertical limit (Morrissey 1980;

Bull 1982). Coral abundance and species richness was significantly higher on the lower reef flat at the northern extent of the reef (41% mean cover, 26 species), and decreased towards the southern extent (9% mean cover, 13 species). This is attributed to a notable decrease in fine sediments at the northern extent, combined with a higher proportion of coral rock and rubble, and the presence of small tide pools with standing water (Table 1). High levels of fine sedimentation on substrates are not conducive to coral recruitment and growth (Rogers 1990; Rogers *et al.* 1994). It is postulated that predominant north-westerly tidal movement drives local cross-shore transport of finer sediment from north to south.

The coral species and lifeforms in these extreme conditions are characteristic of those that occupy sheltered reefs with high sedimentation and turbidity (Rosen 1971; Chappel 1980; Done 1982). Species with massive, submassive and encrusting life forms are more tolerant to thermal stress (Marshall & Baird 2000), while convex and steep sided growth morphologies facilitate sediment flow off surfaces (Lasker 1980; Rogers 1990). The most diverse species were from the Merulinidae, which are represented by species that are tolerant of thermal stress (Depczynski *et al.* 2013; Schoepf *et al.* 2015) and well defined association with turbid water and lengthy periods of emersion. Corals with large polyps, like most species from the Merulinidae are efficient at removing sediment (Marshall & Orr 1931), and species such as *Dipastrea spp.*, *Goniastrea spp*, *Lobophyllia hemphrichii*, *Astrea curta*, *Platygyra* spp., and *Symphyllia recta* can easily manipulate silt and fine sands (Stafford-Smith & Ormond 1992). Species of the genera *Coelastrea and Goniastrea*, for example, are often found in conditions where corals may not be expected to survive (Veron 1986) and are dominant in high latitude reefs in waters of high nutrients and turbidity (Thomson & Frisch 2010). In the Arabian Gulf region, the Merulinidae has a greater representation of species compared to other coral families such as Acroporidae which has greater species diversity in the Indo-Pacific region (Coles 1993; Foster & Foster 2013).

Species of the Acroporidae were scarce, with only two species represented at very low coral cover. The Acroporidae is reported to occur in other regions with high thermal stress (e.g. Craig *et al.* 2001; Bauman *et al.* 2013b; Dandan *et al.* 2015; Schoepf *et al.* 2015). At Nightcliff Reef it is probably further limited by the high turbidity as it is a poor sediment rejector with small polyps less than 2 mm diameter (Stafford-Smith & Ormond, 1992). However, a small-polyped species, *Porites* cf. *nigrescens* (Poritidae) was abundant on the middle and outer reef zones. This species has also been recorded as abundant amongst a coral community surveyed at Cobourg Peninsula, Northern Territory (Billyard 1995) and to the west on macro-tidal reef flats and lagoons off Sunday Island at the mouth of King Sound, Western Australia (Dobson 1999). In further regions, *Porities nigrescens* is reported as common on turbid fringing reefs to the south of Saudi Arabia (Jeddah to Jizan), but disappears to the north in clearer waters (Sheppard 1985). The species is regarded as a shallow water reef builder in environments with low light intensities and low wave energy (Cabioch *et al.* 1999). In northern Australia it appears to have adopted a similar niche to that occupied by *Montipora digitata* that is common on more sedimented inshore reefs of eastern Australia, such as the reef flats of Magnetic Island, Queensland (Bull 1982; Mapstone *et al.* 1992).

Sediments for the upper and middle reef flat zones across the majority of localities were predominantly muds and silts on rock with intervening patches of muddy sand. Benthic algae were both more abundant and more diversely represented in these zones and collectively contributed to 38 species (Table 1). The brown foliose species *Padina australis* dominated the upper reef flat zone. Other conspicuous bladed foliose algae included Sargassacea holdfasts (probably *Sargassopsis decurrens*), *Splatoglossum asperum* and *Dictyopteris* sp. Considerable turf forming algae were also present on the upper reef flat zone, and dominated in the middle reef flat zone with *Amphiroa fragilissima*, *Portieria hornemanni*, *Tricleocarpa fragilis*. *Acanthophora specifera*, *Gracilaria salicornia* and *Anadyomene plicata* visually conspicuous and varying in relative abundance across localities.

The lower reef flat zone, which was dominated by corals, exhibited minimal algal cover (0.03–0.05% mean cover, Table 1). There was no evidence of competition from algae with corals as described in eastern Australia (Morrisey 1980), the Arabian Gulf (Sheppard *et al.* 1992) and the Red Sea (Loya 1977b). It appears corals have a competitive advantage in this lower reef flat zone due to the greater water depth and ability to cope with the high turbidity which results in lower light availability to benthic algae. In the shallower upper tidal zones, longer and more frequent emerison times exclude most coral species, and this allows rapid colonisation of benthic algae which also gain improved light attenuation for photosynthesis.

The algal species recorded at Nightcliff Reef have been widely reported across the Indo-Pacific, from Tanzania (Jassund, 1976) to eastern Australia (Morrissey 1980; Ngan & Price 1980). The abundance of benthic algal species at Nightcliff Reef is likely to be seasonal with species exhibiting variable growth and dominance between wet and dry seasons (e.g. Benayahu & Loya 1977b; Lawson & John 1987; Vuki & Price 1994). The dominance of fleshy brown algae in the upper reef flat zone, with the co–occurrence of turfing algae is similar to the reef flat zonation described in the Gulf of Eilat, Red Sea (Benayahu & Loya 1977a, 1977b).

A notable observation was the limited representation of erect coralline algae from the genus *Halimeda* which is an important contributor to calcium carbonate accretion and grows abundantly on reef flats in eastern Australia (Morrissey 1980), Guam (Merten 1971) and the Gulf of Mannar, India (Rao 1972). However, in similar extreme environmental conditions such as the Arabian Gulf region, *Halimeda* is not recognised as a major component of inshore reefs (Sheppard 1985; Sheppard *et al.* 1992).

The coral species of Darwin Harbour offer valuable insights to physiological and evolutionary adaptations to persist in the most extreme environmental conditions. It is evident from this study and comparative investigations elsewhere that species with large polyps, thick skeletal tissue and massive or submassive lifeform strategies are amongst the most successful to surviving high sedimentation, nutrients and water temperatures.

The close proximity of Nightcliff Reef to coastal development, land–based sources of pollution and marine development combined with the changing climate pose future conservation challenges for this reef which is currently deemed at high risk to integrated local threatening processes (Burke *et al.* 2011).

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